Life History Studies of the Estuarine Nudibranch *Tenellia fuscata* (Gould, 1870)

BY

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INTRODUCTION

THE SMALL AEOLID nudibranch *Tenellia fuscata* (Gould, 1870) can occur in large numbers on concentrations of hydroids in New England estuarine environments (CHAMBERS, 1934; CLARK, 1975). CLARK (*op. cit.*) reported that *T. fuscata* had THOMPSON'S (1967) type 2 or lecithotrophic development and that veligers settled and underwent metamorphosis shortly after hatching.

RASMUSSEN (1944), working with the closely related *Embletonia pallida* Alder and Hancock, 1854 (=*Tenellia adspersa* Nordmann, 1845) reported two developmental patterns at two sites in a Danish estuary; the differences were related to salinity and temperature: At 12‰ and 17.5° C many veligers metamorphosed within the egg capsule and crawled out of the egg mass as vermiform larvae or they hatched as veligers and metamorphosed shortly thereafter. At 20‰ and an average temperature of 22.5° C many veligers swam around for 30 to 120 hours before settling. ROGINSKAYA (1970) reviewed the ecology of *T. adspersa* and stated that populations in the Asov Sea at 12‰ salinity have contained development.

The purpose of this study was to determine the effects of salinity and temperature on the developmental pattern in *Tenellia fuscata*. Cultivation of this euryhaline, eurythermal species was attempted at 4 salinities (5, 10, 20, and 30‰) and 3 temperatures (4°, 13°, and 20° C). Data were collected on the development times and types, growth and fecundity rates and life spans.

MATERIAL AND METHODS

The experimental animals were the F_1 progeny of individuals collected from the Great Bay Estuary (New Hampshire) and a marina in Beverly, Massachusetts. They were maintained in 10 cm diameter stacking dishes and fed the euryhaline hydroid *Cordylophora lacustris* (Allman, 1844), collected at the base of the Oyster River Dam in Durham, New Hampshire. The hydroids were cultured on glass slides held in plastic trays in aquaria at a salinity of 16‰; they were fed nauplii of *Artemia salina* (Linnaeus, 1755).

Replicate experiments were performed at 4 salinities, 5, 10, 20, and 30‰, in three temperature regimes 4° C, 13° C and at room temperature (about 20° C). Pairs of individuals were isolated in 5 cm diameter finger bowls throughout their life cycle. Water was changed daily; in order to reduce thermal shock at lower temperatures, stock solutions were maintained at the desired temperatures.

Daily observations were made with a binocular dissecting microscope equipped with an ocular micrometer. The measurements made included body length, egg mass number, egg number, and developmental stage. To obtain information on rates of development and larval type, individual egg masses were isolated and observed daily.

RESULTS AND OBSERVATIONS

The results of the life cycle studies are summarized in Table 1. The complete life cycle from egg to reproducing adults was observed at all 4 salinities at 20° C. The nudibranchs did best at 20° C and at 30‰ salinity. The second best results were obtained at 20‰ salinity at 20° C. The results at 13 and 4° C were poor, though this may have been due to laboratory conditions rather than *Tenellia fuscata*'s inability to survive under these physical conditions. The results of studies at 20° C and 30‰ salinity will be described and then compared to those at other salinities and temperatures.

At 20° C and 30‰ salinity the life cycle of *Tenellia* from egg laying to death averaged 30 days. It was slightly less at 10‰ salinity (27 days) and at 5‰ salinity (28 days) at 20° C. Animals did not survive well at the other temperatures, particularly at 4° C. The generation time for

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Table 1

Summary of life history data and fecundity information for *Tenellia fuscata* grown at several temperatures and salinities.

Temperature	20°C					13°C			
Salinity	30 ppt		20 ppt		10 ppt	5 ppt	30 ppt	20 ppt	10 ppt
	$F_1(4)$[1]	$F_2(8)$	$F_1(4)$	$F_2(8)$	$F_1(8)$	$F_1(8)$	$F_1(2)$	$F_1(2)$	$F_1(2)$
Time (days) to:									
hatching		5	—	5	6	8-9	12	13	11
metamorphosis		5-6	—	5-6	6-7	9	13	14	12
1st egg mass		20	21	18	16-17	18			
death		31	33	31	27	28			
Length (mm) at:									
veliger		0.125	0.125	0.125	0.125	0.125			
vermiform stage		0.345	—	0.275	0.25	0.31			
1st egg mass		4.35	4.47	4.04	3.85	3.92			
25th day		4.90	4.90	5.17	5.04	4.14			
death		4.40	4.69	4.67	4.75	3.97			
Largest size	7.35 mm		5.59 mm		5.61 mm	4.37 mm			
% Increase in length/day from:									
metamorphosis to 1st egg mass		6.14	—	10.35	9.35	10.23			
1st egg mass to 25th day		2.24	2.19	3.64	2.62	.759			
25th day to death		−1.89	−0.56	−1.78	−3.05	−1.43			
Average fecundity per individual	2686.51	681.5	2073	1246	1014.5	79	374	417	289
Average # of eggs per egg mass	38.11	34.08	47.65	23.07	29.92	9.88	51	40	53
Number of egg masses per individual	70.5	20	43.50	54	35	8	7.3	10.4	5.5
Average # of egg masses per day	5.22	4	6.2	6.75	5.95	3.2	3.5	3.67	3
Egg Size (mm)	0.125	0.125	0.125	0.125					

[1] = Number of individuals observed.

Tenellia was 20 days from egg to egg at 30‰ salinity and it was slightly faster at the lower salinities.

Growth rates from metamorphosis to death in *Tenellia* showed three phases (Table 1). The animals grew very fast, increasing their length by 6-10% per day from the time of metamorphosis to the time the first egg mass was produced. At that point the growth rate decreased to approximately 2% per day until day 25, a time in which animals were at or near the greatest length they would achieve. From day 25 to the time of death, approximately day 31, the growth rate was negative with the animal decreasing in overall length by a few tenths of a millimeter. This trend was consistent at all four salinities at 20 C. No growth rate information was obtained for the other two temperature regimes.

The fecundity of *Tenellia fuscata* is quite high considering the size of the animal and the size of the eggs (Table 1). In the F_1 generation at 20° and 30‰ salinity animals produced almost 2 700 eggs per individual. This was reduced in the F_2 generation to approximately 680 eggs per individual. The number of egg masses per individual per day was slightly over 5 in the F_1 generation and 4 in the F_2 generation. The average number of eggs per spawn was 38 and 34 respectively in the two generations. The largest variable between these two generations at 30‰ salinity was in the total number of egg masses produced per individual, 70 in the F_1 and 20 in the F_2. The fecundity in the F_1 and F_2 generations at 20‰ salinity and 20° C were somewhat similar, though the F_1 had a lower fecundity than at 30‰ and the F_2 a higher fecundity than the F_2 at

30‰. The number of egg masses per day was higher in both the F_1 and F_2 generations at 20‰ salinity though the total number of egg masses was lower than that for the F_1 generation at 30‰. At 10‰ salinity the fecundity was within the range of variation found at the 2 higher salinities. The fecundity at 5‰ salinity was much lower than at the higher salinities; also, none of the eggs developed at this salinity.

There was a slowdown in development time from approximately 5-6 days from egg-laying to metamorphosis at 30 and 20‰ to 8-9 days at 5‰ salinity. At 13° C the development time was approximately 12-14 days at 30, 20 and 10‰. At 4° C no animals were observed to complete development; one egg mass was placed at 4° at the two-cell stage; it took two months for the embryos to reach the 12 cell stage. Shortly thereafter the embryos died. Also, adult *Tenellia fuscata* maintained at 4° C did very poorly, seldom fed and showed little or no growth.

One of the initial areas of interest was developmental type. At all salinities and temperatures where development did occur it was Type 2 development of Thompson (1967) or lecithotrophic. The sequence through to pedi-veliger stage and metamorphosis to the vermiform stage took place whether the animals were within the egg capsule or out swimming and crawling. There was no indication of a factor required to induce metamorphosis. If the stroma of the egg mass was broken down early, then the veligers hatched before the propodium had developed and actively swam. The veligers were rather inactive, spending much of their time on the bottom. After the propodium had formed on day five or later, depending on the salinity and temperature, the animals were then observed to swim and crawl intermittently. By day six at 20° C and 30‰ salinity, the animals had completed metamorphosis and were found only on the stems of the *Cordylophora* provided as food. Therefore, the determining factor in whether the veligers were pelagic for any period of time appeared to be the time taken for the stroma of the egg mass to break down, which released the egg capsules and initiated hatching behavior in the veligers.

The stock culture of *Tenellia fuscata* was initially maintained at 13° C and 30‰ salinity but with the success of cultivation at 20° C and 30‰ most animals used for the later experiments were derived from animals maintained at the latter temperature and salinity. Egg masses containing uncleaved zygotes or embryos in the early cleavage stages were incapable of surviving transfer to lower salinities whether it be from 30‰ to 20‰ or 20‰ to 10‰ or 10‰ to 5‰. Embryos were able to survive salinity changes only after they had begun rotating within the egg capsules. In all cases, metamorphosed nudibranchs were better able to survive changes in salinity than were developing veligers.

At the lowest salinities, 10‰ and 5‰, survival was poor both among larvae and adults transferred from higher salinities. Embryos transferred to these salinities showed high mortality and those that did continue to develop tended to have abnormal appearing shells. However, abnormal shells did not inhibit survival and metamorphosis was completed in these individuals. At 10‰ salinity eggs laid by the individuals in that culture developed, but did not survive to metamorphosis. At 5‰ none of the eggs produced by the one pair raised at this salinity began to cleave.

DISCUSSION

The results of this study suggest that *Tenellia fuscata* does best at higher salinities and temperatures. Field collections from the Great Bay Estuary indicated that the appearance of this nudibranch at sites within the estuary corresponded with the appearance of certain hydroid species and the nudibranchs were observed farther up the estuary as salinities and temperatures increased.

The Great Bay Estuarine System has a wide range in salinity and temperature. Salinities in the upper bay fluctuate from about 5‰ during the spring thaw to 32‰ in late summer. Temperatures range from —1.5° C in late winter to about 27° C in August. Hydroid species found in the estuary tend to show a sequential appearance keyed to temperature and salinity conditions (Normandeau, 1976). The short life cycle and high fecundity in *Tenellia fuscata* are obvious adaptations for exploiting a transient food source (Miller, 1961, 1962; Thompson, 1964).

Tenellia fuscata has an ecology similar to that described for *T. adspersa* (Rasmussen, 1944; Roginskaya, 1970), though it does not seem to have a high tolerance for low salinities. The lowest salinity recorded by Clark (1975) was 16‰ while 20‰ was the minimum salinity recorded at collection sites during this study. Rasmussen (1944) found *T. adspersa* at 12‰ and it is reported in salinities down to 5‰ (Roginskaya, 1970). At 20° C adult nudibranchs did survive and reproduce at salinities of 10‰ and 5‰, but the development of embryos was incomplete (10‰) or no development occurred (5‰).

Before the experiments began, *Tenellia* were maintained at 13° C and 30‰ salinity. Under these conditions sur-

vival, growth and reproduction were excellent, so the poor results at this temperature during the experiments was surprising. Most of the experiments at the lower temperatures were attempted during the time when there was trouble with toxic substances diffusing from plastic culture trays and the *Cordylophora* was doing poorly. The unhealthy hydroid food may have affected the well-being of the nudibranchs.

One of the primary goals of this study was to see if changing temperatures or salinities or both would affect development type as suggested by RASMUSSEN (1944). Rasmussen found that *Tenellia adspersa* at 22.5‰ salinity and 20-25° C hatched in 4 days and swam about for 30 to 120 hours before undergoing metamorphosis while at 12‰ salinity and 17° C the veligers metamorphosed before leaving the egg mass at 9 days. In both cases metamorphosis was complete by 9 days and hatching time was the primary difference. The 5 to 9 days development to metamorphosis at the higher temperature and salinity is comparable to the results at 20° C and 20‰ and 30‰ in this study, while the 9 days to metamorphosis at hatching at the lower salinity and temperature is faster than that observed at 13° C and 20‰ (14 days). Therefore, while development time and pattern did not vary in *T. adspersa,* temperature and salinity do appear to influence the rate of development in *T. fuscata.* The influence of temperature and salinity on the physiology of animals is well documented (NEWELL, 1970). In this study, the development times at 20° C and 30‰, 20‰, 10‰, and 5‰ were 6, 6, 7 and 9 days respectively, suggesting that salinity, independent of temperature, can influence the developmental rate,at least in *T. fuscata.*

The second factor that appears to be important here is the rate of breakdown of the stroma of the egg mass. Veligers will not attempt to hatch from their capsules until the gelatinous matrix of the egg mass has broken down sufficiently to release the capsules (HARRIS, 1973). If the stroma does not break down, the veligers continue development through metamorphosis and hatch in the vermiform stage. Evidence from this study and previous experience by the senior author (HARRIS, 1973, 1975) indicate that external factors such as bacterial action, burrowing by micrometazoa and water motion are primarily responsible for the breakdown of the stroma of nudibranch egg masses. It seems likely that the differences in hatching time for *Tenellia adspersa* observed by RASMUSSEN (1944) were influenced by the rates at which the egg masses broke down at the two salinity and temperature regimes.

One of the more interesting findings of this study was the inability of zygotes and early embryos to tolerate salinity changes. Only after embryos had begun to rotate within the capsules were they able to survive a drop in salinity. An organism living within a fouling community at a fixed point in an estuary does not experience a single temperature or salinity on a tidal cycle,but rather a range of salinities and temperatures. An animal may not be able to survive permanently at one of the extremes of this range, but it may be able to endure short exposures as long as the remainder of the time the environmental conditions are well within its range of tolerance. It was found that *Tenellia* grown at one salinity produced eggs that were not able to adjust to a drop in salinity though early veligers were capable of osmoregulating. It would be interesting to see if adult *Tenellia* exposed to a cyclical range of salinities produced eggs with a greater tolerance to salinity fluctuation. If one is to understand the ecology and physiological adaptiveness of estuarine organisms, these must be tested under conditions similar to the actual fluctuating environment in which they typically occur.

SUMMARY

1. The estuarine aeolid nudibranch *Tenellia fuscata* was raised under laboratory conditions to compare several aspects of its life cycle when grown at various temperature (20, 13, and 4° C) and salinity (30, 20, 10, and 5‰) regimes. The parameters compared included growth rate, generation time, fecundity and development type.

2. Growth and survival were best at 30 and 20‰ salinities at 20° C. Development time from egg laying to metamorphosis increased at 10 and 5‰ at 20° C and also at the lower temperatures.

3. There was no difference in the development type; variation in the stage at which the young nudibranchs hatched was dependent on the rate at which the stroma of the egg mass deteriorated.

4. Eggs and embryos were not able to tolerate decreases in salinity until they were rotating in the egg capsule. It was suggested that, since estuarine forms experience a constantly fluctuating environment, tolerance levels might be best understood if they were studied using a system that mimicked the natural fluctuating environment.

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